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A STATISTICAL ANALYSIS OF FACTORS ASSOCIATED WITH HISTORICAL EXTINCTION AND CURRENT ENDANGERMENT OF NON-PASSERINE BIRDS

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ABSTRACT.—Data on historical extinction and current endangerment in non-passerine birds were used to assess associations between vulnerability to human impacts and genus size, range size, and insular endemism. Consistent with the results of previous studies, historical extinction was more frequent in species from monotypic genera, even when other factors were controlled for statistically. By contrast, current endangerment showed no such pattern when other factors were controlled for. Both historical extinction and current endangerment were more frequent in species with restricted ranges and for insular species. Moreover, insular species with restricted ranges were especially vulnerable to current endangerment. Changes between the patterns of historical extinction and current endangerment are likely due to changes in the nature of human impacts over the past 500 years, especially the recent trend toward wholesale habitat destruction. *Received 27 August 2003, accepted 20 September 2004.*

At the present time, the earth's biota is facing an anthropogenic, mass extinction event, unique in the history of our planet (Diamond 1989). It is difficult to predict the ultimate impact of this extinction event, but an analysis of the patterns of recent extinction and current endangerment may enable us to determine trends that will suggest strategies for minimizing the damage (Pimm et al. 1988, Smith et al. 1993, Bibby 1995, Gaston and Blackburn 1997, McKinney and Lockwood 1999, Balmford et al. 2003). Nee and May (1997) showed that a pattern of random extinctions across a phylogeny will conserve nearly as much of the evolutionary history represented by the species in that phylogeny as a strategy explicitly designed to preserve as much of that evolutionary history as possible. This finding may provide hope that the loss of genetic information will be relatively minor.

On the other hand, numerous studies of patterns of historical extinction and recent endangerment in birds and mammals have shown that human impacts on these taxa are far from random, relative to phylogeny (Russell et al. 1998, Hughes 1999, Purvis et al. 2000, von Euler 2001). Those studies have revealed that both historical extinction and recent endangerment have disproportionately affected genera that contain few species, particularly monotypic genera (Russell et al. 1998, Hughes 1999, Purvis et al. 2000). Assuming that taxonomic classifications at least approximately reflect genetic relationships, such a pattern may suggest a disproportionate human impact on species without close relatives or with few close relatives.

The results of these studies, however, did not clarify the mechanisms behind the apparent tendency of human activities to have greater impacts on species with few or no close relatives. It is possible that some other variable is correlated with scarcity of close relatives. For example, it is well known that human impact has been particularly severe on insular species of birds and certain other groups of organisms (Cronk 1997). Because many insular species have evolved in relative isolation and are thus often assigned to monotypic or species-poor genera, the observed effect may in fact reflect nothing more than the overall vulnerability of insular species.

Russell et al. (1998) and Hughes (1999) compared patterns of historical extinction (since European expansion, beginning in the 15th century) with current patterns of endangerment in order to assess changes in the pattern of human impacts. One of the most striking changes was found in non-passerine birds (Hughes 1999). In both non-passerine and passerine birds, the proportion of historical extinctions was found to be significantly greater in monotypic genera than in polytypic genera. Similarly, in passerines, the proportion of current endangerment was found to be higher in monotypic than in polytypic genera.

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However, in non-passerines, where proportions of both historical extinction and current endangerment were found to be substantially higher than in passerines, there was no difference between monotypic and polytypic genera with respect to rate of current endangerment (Hughes 1999). These results suggest that the nature of human impacts on non-passerine bird species recently changed—from differential impacts on species without close relatives to "across-the-board" impacts.

Here, I analyze data on proportions of historical extinction and current endangerment in non-passerine birds to assess the factors underlying observed patterns. First, I assess the contribution of insularity, restricted range, and genus size to extinction and endangerment, testing for independent effects of each of these factors while controlling statistically for the other factors. Second, I compare the incidence of historical extinction and current endangerment to test the hypothesis that there has been a recent fundamental change in the nature of human impacts on the survival of non-passerine bird species.

METHODS

Analyses were based on data for 3,966 species of non-passerine birds. Species and higher-level taxonomies were based on those recognized by Sibley and Monroe (1990, 1993), including more recently described species recognized by Collar et al. (1994) and Stattersfield et al. (1998). The number of species included in the analysis differs from that in Hughes (1999) because of the addition of three species recognized by Collar et al. (1994) and Stattersfield et al. (1998). Historical extinction was defined as extinction occurring since European expansion (15th century until present). Species were classified as extinct following Sibley and Monroe (1990, 1993), although I also considered the California Condor (*Gymnogyps californianus*; extinct in the wild) as extinct on the grounds that my study emphasizes impacts on natural populations. Any species classified as vulnerable, endangered, or critical by Collar et al. (1994) was classified as currently endangered. Species were classified as insular if their life cycle includes no continental phase. Thus, species whose life cycle involves migration between an island and a continent were not classified as insular; pelagic feeders breeding exclusively on islands were classified as insular.

I defined restricted-range landbirds as those whose total global breeding range since 1800 was estimated by Stattersfield et al. (1998) to be $\leq$50,000 km^2; however, any species whose current range is $\leq$50,000 km^2, but was $>$50,000 km^2 at any point since 1800 (Stattersfield et al. 1998), was not counted as a restricted-range species. For a given species, the range size was defined as the area contained within an imaginary boundary (or boundaries, in the case of discontinuous ranges) encompassing all known or inferred sites of occurrence (Stattersfield et al. 1998).

I analyzed data in the form of two $2 \times 2 \times 2 \times 2$ contingency tables. In the first of these tables, all species, whether extant or extinct, were included. I classified species according to four variables: genus size (monotypic, polytypic), insularity (insular, continental), range size (restricted range, non-restricted range), and historical extinction (extinct, non-extinct). The second contingency table included only extant species, which were classified according to four variables: genus size (monotypic, polytypic), insularity (insular, continental), range size (restricted range, non-restricted range), and current endangerment (endangered, non-endangered). Using log-linear models (Everitt 1977), I tested for partial association between extinction and each of the other three variables while statistically controlling for the other two variables. Similarly, in the data set of extant species, I tested for partial association between endangerment and each of the other three variables, statistically controlling for the other two variables. Similar analyses were applied separately to eight families of non-passerine birds (Anatidae, Phasianidae, Rallidae, Columbidae, Psittacidae, Strigidae, Trochilidae, and Picidae). These families were chosen because each included a substantial number of species ($\geq$143 species), one or more endangered species, and one or more extinct species.

RESULTS

The proportions of non-endangered, endangered, and extinct species appeared similar in polytypic and monotypic genera (Fig. 1). The major difference was a higher proportion of extinct species among monotypic (2.4%) than

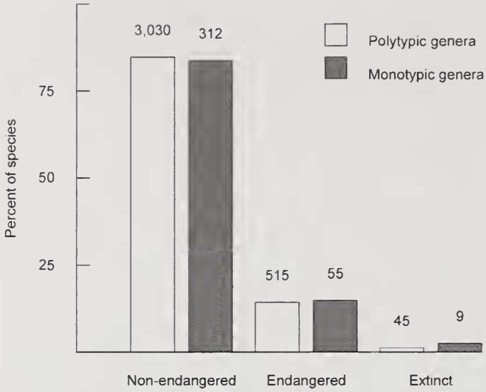

FIG. 1. Percentages of non-passerine species belonging to polytypic and monotypic genera classified as non-endangered, endangered, and extinct. Numbers of species are given above each bar.

among polytypic (1.3%) genera. The partial test of association between genus size and historical extinction was highly significant (P = 0.006; all non-passerines; Table 1). However, there was no significant association between genus size and current endangerment (Table 2).

In monotypic but not in polytypic genera, the proportion of extinction was higher in insular than in continental species (Fig. 2). And in both monotypic and polytypic genera, the proportion of endangerment was higher in insular than in continental species (Fig. 2). Log-linear analyses showed a highly significant partial association (all non-passerines; $P < 0.001$) between insularity and both extinction (Table 1) and endangerment (Table 2). Similarly, the proportions of both extinction and endangerment in both polytypic and monotypic genera were higher in restricted-range species than in other species (Fig. 3). Again, log-linear analyses showed a highly significant association between range size and extinction ($P < 0.001$; Table 1) and between range size and endangerment ($P < 0.001$; Table 2).

In log-linear analyses examining all non-passerines for associations with historical extinction, there were no significant ($P < 0.05$) two-way interactions between any pair of variables (Table 1). By contrast, the analysis of current endangerment revealed a highly significant interaction between insularity and range size (Table 2; Fig. 4). Among endangered continental species, non-restricted range species (141 of 287 or 49.8%) and restricted-range species (146 of 287 or 50.2%) accounted for nearly equal percentages of species (Fig. 4). Among endangered insular species, however, the proportion of restricted-range species (195 of 283 or 68.9%) was more than twice that of non-restricted range species (88 of 283 or 31.1%; Fig. 4).

None of the individual families showed a significant partial association between extinction and range size (Table 1). In Psittacidae, there were significant partial associations between extinction and both genus size and insularity (Table 1). In Anatidae and Columbidae, there was a significant partial association between extinction and genus size but not between extinction and insularity (Table 1). On the other hand, in Phasianidae, Rallidae, Trochilidae, and Picidae, there was a significant

TABLE 1. Significance levels for tests of partial association between historical extinction and genus size, insularity, and range size in eight families of non-passerine birds and in all non-passerines.[a]

Family	Number of species	Genus size	Insularity	Range size	Genus size × insularity[b]	Genus size × range size[b]	Insularity × range size[b]
Anatidae	148	0.044	NS[c]	NS	NS	NS	NS
Phasianidae	177	NS	0.017	NS	NS	NS	NS
Rallidae	143	NS	0.008	NS	NS	NS	NS
Columbidae	313	0.008	NS	NS	NS	NS	NS
Psittacidae	360	0.008	0.028	NS	NS	NS	NS
Strigidae	143	NS	NS	NS	NS	NS	NS
Trochilidae	324	NS	0.003	NS	NS	NS	NS
Picidae	216	NS	0.017	NS	NS	NS	NS
All non-passerines	3,966	0.006	<0.001	<0.001	NS	NS	NS

[a] Entries are P-values for tests of partial association based on log-linear models.
[b] Two-way interactions.
[c] NS = not significant ($P > 0.05$).

TABLE 2. Significance levels for tests of partial association between current endangerment and genus size, insularity, and range size in eight families of non-passerine birds and in all non-passerines.[a]

Family	Number of species	Genus size	Insularity	Range size	Genus size × insularity[b]	Genus size × range size[b]	Insularity × range size[b]
Anatidae	146	NS[c]	0.009	0.035	NS	NS	NS
Phasianidae	176	NS	0.025	<0.001	NS	NS	<0.001
Rallidae	130	NS	NS	<0.001	NS	NS	NS
Columbidae	307	NS	NS	<0.001	NS	NS	NS
Psittacidae	347	NS	NS	<0.001	NS	NS	NS
Strigidae	141	NS	NS	<0.001	NS	NS	NS
Trochilidae	323	NS	NS	<0.001	NS	NS	NS
Picidae	214	NS	NS	NS	NS	NS	NS
All non-passerines	3,912	NS	<0.001	<0.001	NS	NS	<0.001

[a] Entries are P-values for tests of partial association based on log-linear models.
[b] Two-way interactions.
[c] NS = not significant ($P > 0.05$).

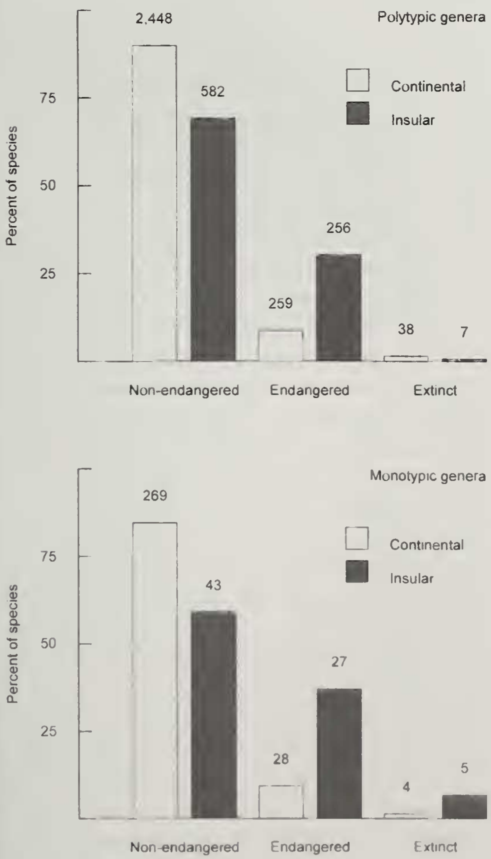

FIG. 2. Percentages of continental and insular non-passerine species classified as non-endangered, endangered, and extinct. Numbers of species are given above each bar.

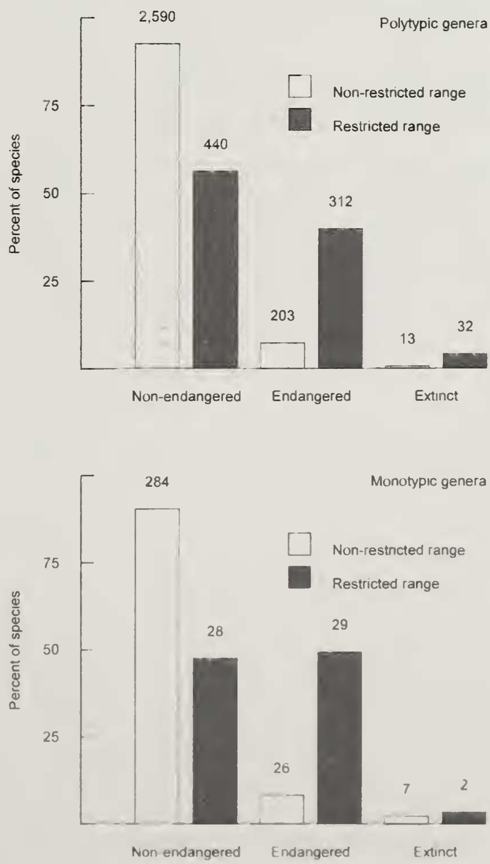

FIG. 3. Percentages of non-restricted range and restricted range non-passerine species classified as non-endangered, endangered, and extinct. Numbers of species are given above each bar.

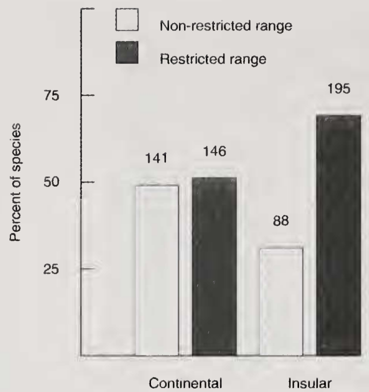

FIG. 4. Percentages of non-restricted range and restricted-range endangered, non-passerine species classified as continental or insular. Numbers of species are given above each bar.

partial association between extinction and insularity but not between extinction and genus size (Table 1). In the analysis of extinction, none of the eight families showed any significant two-way interactions (Table 1).

None of the eight families showed a significant partial association between endangerment and genus size (Table 2). Only Anatidae and Phasianidae showed significant partial associations between endangerment and insularity, whereas all families except Picidae showed significant partial associations between endangerment and range size (Table 2). There was a significant interaction between insularity and range size only in Phasianidae (Table 2). Picidae was unique in showing no significant partial associations with endangerment or two-way interactions (Table 2).

Several authors have noted that the analysis of factors affecting extinction and endangerment may be improved by taking into account autocorrelation between phylogenetically close species (Lockwood et al. 2002, Cassey et al. 2004). In the absence of a phylogeny, Cassey et al. (2004) based autocorrelations on taxonomic categories. To test for effects of taxonomic category, I combined the data from the eight families listed in Tables 1 and 2 and included family as an additional category in the log-linear analysis. None of the effects listed in Tables 1 and 2 showed a significant partial interaction with family, implying that differences among families were not a significant factor in the results reported here.

DISCUSSION

With respect to non-passerine birds, the results reported here are consistent with earlier results (Hughes 1999)—showing both a significantly higher proportion of historical extinctions in monotypic genera and no difference between proportions of current endangerment in monotypic and polytypic genera. Furthermore, these patterns hold true even when the effects of insularity and range size are controlled for statistically. The results support the hypothesis that historic extinction has disproportionately affected non-passerine bird species belonging to monotypic genera regardless of insularity and range size (Table 1). On the other hand, there was no significant association between current endangerment and genus size when the effects of insularity and range size were controlled for (Table 2).

One reason for this difference may be that the most vulnerable non-passerines belonging to monotypic genera have already been driven to extinction (Hughes 1999). The situation is quite different among passerines; the proportion of historical extinctions is considerably lower than that of non-passerines, and currently endangered passerines include a significantly higher proportion of species belonging to monotypic genera than do non-endangered passerines (Hughes 1999). An additional factor may be that historical extinctions of non-passerine species in monotypic genera have included some species with unusual characteristics. For example, extinct non-passerines from monotypic genera include four continental species with very broad ranges: Pink-headed Duck (*Rhodonessa caryophyllacea*), Passenger Pigeon (*Ectopistes migratorius*), Carolina Parakeet (*Conuropsis carolinensis*), and California Condor. These species represent 44% (4 of 9) of all extinct species from monotypic genera. By contrast, only 27.3% (15 of 55) of currently endangered species from monotypic genera are continental species with non-restricted ranges. Thus, one major change has been the loss of a set of geographically widespread but uniquely vulnerable continental species. In the absence of these species, range size and insular endemism have become increasingly important factors in predicting vulnerability.

In contrast to the results for genus size, both historical extinction and current endangerment were significantly associated with both range size and insularity, even when other variables were controlled for statistically (Tables 1 and 2). The association with range size is not unexpected, since range size is a factor that goes into the assessment of endangered status (Collar et al. 1994). However, the estimates of range size used here were based on historical ranges; thus, some species with currently limited ranges were not scored as "restricted-range" species (Stattersfield et al. 1998). An association between insularity and both extinction and endangerment was hypothesized by Russell et al. (1998) and Hughes (1999), and the present results support this hypothesis.

Nonetheless, there was a striking difference between the results for historical extinction and those for current endangerment when the effect of range size was examined separately for different families. In the case of historical extinction, separate examination of each of eight non-passerine families showed no significant effects of range size (Table 1). By contrast, seven of eight families showed a significant partial association between range size and current endangerment, and in six of these families the association was highly significant (Table 2). These results suggest that non-passerine species with restricted ranges are becoming increasingly vulnerable to human impacts, independent of other factors and in a similar manner across taxonomic categories.

There was a significant interaction between range size and insularity for currently endangered species but not for extinct species (Tables 1 and 2). This interaction is explained by the much higher proportion of restricted-range species that are insular compared with the proportion of restricted-range species that are continental (Fig. 4). This in turn implies that insular species are now doubly vulnerable—by virtue of both their insular distribution and their range size. The absence of such a pattern in the data on historical extinction suggests that this is a new phenomenon, resulting from recent changes in the nature of human impacts. It seems likely that these changes include a trend toward wholesale habitat destruction (Owens and Bennett 2000), to which restricted-range species—especially those on islands—are especially vulnerable.

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LITERATURE CITED

Balmford, A., R. E. Green, and M. Jenkins. 2003. Measuring the changing state of nature. Trends in Ecology and Evolution 18:326–330.

Bibby, C. J. 1995. Recent past and future extinctions in birds. Pages 98–110 *in* Extinction rates (J. H. Lawton and R. M. May, Eds.). Oxford University Press, Oxford, United Kingdom.

Cassey, P., T. M. Blackburn, G. J. Russsell, K. E. Jones, and J. L. Lockwood. 2004. Influences on the transport and establishment of exotic bird species: an analysis of the parrots (Psittaciformes) of the world. Global Change Biology 10:417–426.

Collar, N. J., M. J. Crosby, and A. J. Stattersfield. 1994. Birds to watch 2: the world list of threatened birds. International Council for Bird Preservation, Cambridge, United Kingdom.

Cronk, Q. C. B. 1997. Islands: stability, diversity, conservation. Biodiversity and Conservation 61:11–15.

Diamond, J. M. 1989. The present, past, and future of human-caused extinctions. Philosophical Transactions of the Royal Society of London, Series B 325:469–477.

Everitt, B. S. 1977. The analysis of contingency tables. Chapman and Hall, London, United Kingdom.

Gaston, K. J. and T. M. Blackburn. 1997. Evolutionary age and risk of extinction in the global avifauna. Ecology and Evolution 11:557–565.

Hughes, A. L. 1999. Differential human impact on the survival of genetically distinct avian lineages. Bird Conservation International 9:147–154.

Lockwood, J. L., G. J. Russell, J. L. Gittleman, C. C. Daehler, M. L. McKinney, and A. Purvis. 2002. A metric for analyzing taxonomic patterns of extinction risk. Conservation Biology 16:1137–1142.

McKinney, M. L. and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology and Evolution 14:450–453.

Nee, S. and R. M. May. 1997. Extinction and the loss of evolutionary history. Science 278:692–694.

Owens, I. P. F. and P. M. Bennett. 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. Proceedings of the National Academy of Sciences 97: 12144–12148.

Pimm, S. L., H. L. Jones, and J. Diamond. 1988. On the risk of extinction. American Naturalist 132: 757–785.

Purvis, A., P.-M. Agapow, J. L. Gittleman, and G. M. Mace. 2000. Nonrandom extinction and the loss of evolutionary history. Science 288:328–330.

RUSSELL, G. J., T. M. BROOKS, M. M. MCKINNEY, AND C. G. ANDERSON. 1998. Present and future taxonomic selectivity in bird and mammal extinctions. Conservation Biology 12:1365–1376.

SIBLEY, C. G. AND B. L. MONROE, JR. 1990. Distribution and taxonomy of birds of the world. Yale University Press, New Haven, Connecticut.

SIBLEY, C. G. AND B. L. MONROE, JR. 1993. A supplement to distribution and taxonomy of birds of the world. Yale University Press, New Haven, Connecticut.

SMITH, F. D. M., R. M. MAY, R. PELLEW, T. M. JOHNSON, AND K. S. WALTER. 1993. Estimating extinction. Nature 354:494–496.

STATTERSFIELD, A. J., M. J. CROSBY, A. J. LONG, AND D. C. WEGE. 1998. Endemic bird areas of the world: priorities for biodiversity conservation. International Council for Bird Preservation, Cambridge, United Kingdom.

VON EULER, F. 2001. Selective extinction and rapid loss of evolutionary history in the bird fauna. Proceedings of the Royal Society of London, Series B 268:127–130.